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Determining the relative roles of climate and tectonics in the formation of the fossil record of terrestrial vertebrates: a perspective from the Late Cretaceous of western North America

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Abstract – Both climate and tectonics have been demonstrated to be prominent factors in the formation of the sedimentological record. By extension, these factors must have been influential in the preservation of the vertebrate fossil record. The Late Cretaceous Foreland Basin of the Rocky Mountain region in North America is a rich source of vertebrate fossil remains and is ideally situated to investigate this issue. A sample of 185 published and unpublished vertebrate localities has been examined to determine the relative influence of regional tectonism versus climate in the formation of this fossil record.

The localities considered are from the Judith River Formation and Two Medicine Formations of Montana, and the Judith River Group of southern Alberta. These sites were classified as event, attritional, or lag accumulations. A chi-square analysis of the distribution of these types of localities along a proximal-distal transect perpendicular to the long axis of the foreland basin shows that the pattern of fossil preservation is dependent upon location, suggesting that tectonics was the dominant factor in the formation of this fossil record. However, a similar chi-square analysis of sites along a longitudinal transect in the distal regions of the foreland basin also shows that the pattern of fossil preservation is dependent on location. This pattern suggests that regional tectonism had a minor role in the formation of these deposits.

This dependency on location seems to relate closely to the sandstone/mudstone ratios of each region. These ratios are taken as indicators of rates of floodplain aggradation in the individual areas, which is controlled by local tectonism, subsidence and/or climate. Of these three, climate seems the most viable alternative. Based on this statistical analysis, it appears that large-scale tectonism is not a prominent influence in the formation of the vertebrate fossil record in the Late Cretaceous of northern western North America.

INTRODUCTION

There is but one history of past life on this planet, the fossil record. As palaeontologists we are concerned with the patterns of this record and the evolutionary processes that created these patterns (summarized most recently in Carroll 1997). Perhaps just as importantly is an appreciation for what were the large-scale driving forces behind the formation of fossil deposits or, more simply, how did the fossil record form? Given the scope of the issue, this paper will address only the factors affecting the formation of vertebrate-bearing fossil deposits. Also, given that a significant portion of the vertebrate fossil record occurs within fluvial deposits, this study will focus only on such deposits.

A good deal of discussion has been generated describing the local conditions of bonebed formation and the taphonomic parameters of bone assemblages within specific depositional environments (Voorhies 1969; Behrensmeyer 1975; Dodson 1973; Korth 1979; Hunt 1978; Fiorillo 1988a, 1989, 1991a; Blob 1997; Blob and Fiorillo 1996; Maas 1985; Rogers 1990; Henrici and Fiorillo 1993; Varricchio 1995; and many others). Recently it has been suggested by Rogers (1993) that a large-scale tectonic picture controlled the distribution of types of fossil accumulations and the resulting palaeoecological interpretations. Specifically, within the Late Cretaceous Foreland Basin of the northern United States, it has been suggested that a proximal-distal tectonic position determined the type of vertebrate accumulation. In contrast, Brain (1995) has pointed out that climate controlled the completeness of the hominid record in African caves. Similarly, recent work in the famed Cretaceous dinosaur beds of the Gobi Desert has shown that palaeoclimate influenced patterns of sedimentation, and the resulting patterns of fossil preservation (Loope *et al*. 1998).

Because the Late Cretaceous Foreland Basin is so rich in vertebrate remains, the purpose of this review is to investigate this conclusion on a broader

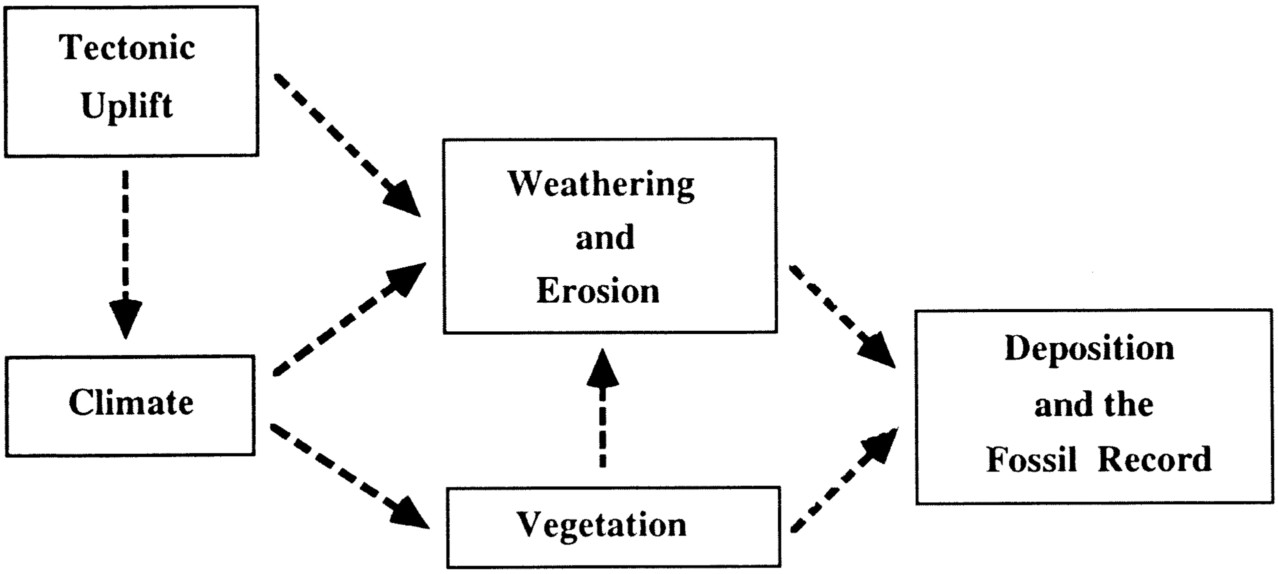

Figure 1 Potential interactions between the various parameters influencing the formation of the vertebrate fossil record in fluvial settings.

scale by expanding the study area and including the world-famous dinosaur-bearing beds of southern Alberta and the vertebrate assemblages of southern Montana. By expanding the area of Rogers' (1993) study, but only by adding sites from the distal margins of the foreland basin, this study will be holding the tectonic variable constant and investigate other factors influencing the taphonomic mode of preservation of vertebrate remains.

Figure 1 illustrates some of the possible factors leading to deposition and the resulting fossil record. Examination of this figure shows that there are several routes that can be traced along which tectonics is the ultimate cause. However, the focus here is to investigate the most direct factors influencing the formation of the fossil record rather than the ultimate factors. Each of these links has been well established through previous work.

For example, Ruddiman and Prell (1997) have summarized the arguments intricately linking uplift and climate, where they define uplift as "raising of Earth's surface across broad plateau or mountain regions". Reference to tectonics in this paper implies this definition. In addition, Milliman (1997) has pointed out the direct role of the topography-tectonic link with sediment discharge, shown in Figure 1 as the block for weathering and erosion. Clearly, climate can influence weathering and erosion rates, independent of vegetative cover (Leopold *et al.* 1964). It is a basic tenet that climate controls vegetative cover (Jenny 1941) and that vegetative cover can influence sediment yield (Leopold *et al.* 1964; Walling 1995, 1996). And with respect to vegetation, even at the small scale, the type of vegetation can influence erosion rates (Keller and Swanson 1979; Keller and Tally 1979; Keller and MacDonald 1995; Smith 1976). The net rates of erosion affect the patterns of deposition and the subsequent fossil record. By holding constant the ultimate cause, tectonics, we can examine the roles of some of these other factors in the formation of the vertebrate fossil record in the Cretaceous Foreland Basin of western North America.

GEOLOGIC, GEOGRAPHIC AND HISTORICAL BACKGROUND OF THE CRETACEOUS FORELAND BASIN OF WESTERN NORTH AMERICA

The Late Cretaceous Foreland Basin of western North America (Figure 2) is filled with several formations. Of these various rock units, two of closely related origin have yielded the vast majority of vertebrate fossil material, the Judith River Formation and the Two Medicine Formation.

The Judith River Formation, a major rock unit throughout much of Montana and southern Canada, is historically important as yielding the first documented dinosaur remains from North America (Leidy 1856). In southern Alberta, this unit has yielded many spectacular dinosaur specimens (Dodson 1971, 1983), and continues to be an active source of fossil remains in both Canada (e.g., Brinkman 1990; Currie *et al.* 1990) and Montana (Sahni 1972; Case 1978; Montellano 1992; Dodson 1986; Fiorillo 1987a, 1987b, 1989, 1991a, 1991b, 1997; Fiorillo and Currie 1994; Blob and Fiorillo 1996). Recently, this unit has been elevated to group status in Canada, based on a major sedimentological change that is traceable over a large geographic area in southern Alberta, Saskatchewan, and northern Montana (Eberth and Hamblin 1993).

Figure 2 Geographic distribution of the Judith River-Two Medicine clastic wedge. Modified from Eberth and Hamblin (1993).

The Two Medicine Formation is a thick rock unit that crops out in northwestern Montana and is laterally equivalent to several formations including the Judith River Formation. This rock unit has also yielded several spectacular dinosaur specimens (e.g. *Brachyceratops* Gilmore, 1917), but has been relatively ignored until much more recently. Renewed interest in this rock unit has shown the Two Medicine Formation to be rich in vertebrate fossil remains (Horner and Makela 1979; Horner 1983; Horner and Weishampel 1988; Rogers 1990; Varricchio 1995).

The tectonic reconstruction of this region during the Campanian is a foreland basin with orogenic activity to the west (Dickinson and Snyder 1978) and an inland sea to the east (Eisbacher *et al.* 1974; Lillegraven and Ostresh 1990). This palaeogeography has yielded a clastic wedge that thickens from only several tens of metres in the eastern extent (Gill and Cobban 1973) to several hundred metres of depth of section in the western extent (Rogers 1994).

MATERIALS AND METHODS

One hundred and eighty-five published and unpublished localities were examined to determine the relative influence of regional tectonism versus climate in the formation of this fossil record. The localities considered are from the Judith River Formation and Two Medicine Formations of Montana, and the Judith River Group of southern Alberta. Published locality data for the Judith River Formation of south-central Montana have been described previously (Blob and Fiorillo 1996; Fiorillo 1987a, 1987b, 1989, 1991a, 1997). In addition to these localities, this study also includes data from unpublished field notes by the author. Details of the localities for the Judith River and Two Medicine Formations of central and northern Montana were obtained from Rogers (1993). Lastly, the locality information for sites in Canada was obtained from Dodson (1971), Brinkman (1990), Eberth (1990), and Wood *et al.* (1988). With respect to palaeogeographic reconstruction, these three areas are approximately 275 to 350 km east of the Fold and Thrust Belt (Lehman 1997).

The sites were classified as event, attritional, or lag accumulations, following Rogers (1993). Such a classification implies varying degrees of time-averaging and resultant palaeoecological interpretation. For example, Rogers (1993) recognized that event accumulations were the result of brief time intervals, such as mass death events. As such, these types of accumulations represent 'snapshots' of an ancient ecosystem (i.e. offer high temporal resolution). In contrast, attritional accumulations represent much longer time intervals and are 'averaged' pictures of an ecosystem (i.e. offer low temporal resolution). This latter accumulation, by incorporating a greater time slice, has a higher probability than an event accumulation of recording migrant taxa as part of an ecosystem. Attritional accumulations are also likely to record faunal changes due to climatic shifts.

RESULTS

The frequencies of these event, attritional, and lag accumulations for the Judith River Formation (= Group) of southern Alberta, northern Montana, and south-central Montana, and the Two Medicine Formation are presented in Table 1, which also includes the sandstone/mudstone ratios of each of these four regions. Data for the chi-square analyses are summarized in Tables 2–4.

Table 1 Summary of types of vertebrate fossil localities in the Judith River Formation – Two Medicine Formation clastic wedge of the Late Cretaceous foreland basin of western North America. Data from Rogers (1993), Dodson (1971), Brinkman (1990), Eberth (1990), Wood *et al.* (1988), Blob and Fiorillo (1996), Fiorillo and Currie (1994), and Fiorillo (1987a, 1987b, 1989, 1991a, 1997), and unpublished field notes of the author. Abbreviations: SCMT = south-central Montana; NCMT = north-central Montana; SAB = southern Alberta.

	Judith River Formation			Two Medicine Formation
Type of Bonebed	SCMT	NCMT	SAB	
Lag	6	10	79	0
Event	6	3	11	24
Attritional	9	7	25	5
Sandstone/Mudstone	.30	.56	.70	.30

Table 2 Observed and expected values for the chi-square analysis to test independence of type of vertebrate fossil locality and geographic location, data from Rogers (1993). The expected values follow, in parentheses, the observed values in the table. The analysis was performed at 5% significance level, with 2 degrees of freedom. The calculated chi-square value is 25.7 and the expected value is 5.9. Because the calculated value is greater than the expected value, the null hypothesis, fossil type is independent of location, is rejected. This suggests that regional geology has an influence on type of fossil locality. Table format follows examples from Rees (1989). NCMT = north-central Montana.

	Judith River Formation	Two Medicine Formation	
Type of bonebed	NCMT		*N*
Lag	10(4.1)	0(5.9)	10
Event	3(11.0)	24(16.0)	27
Attritional	7(4.9)	5(7.1)	12
N	20	29	

The null hypothesis for the chi-square analysis is that the type of bonebed is independent of location. A chi-square analysis (at the 5% level) of the distribution of these types of localities along a proximal-distal transect perpendicular to the long axis of the Foreland Basin shows that the calculated chi-square value is greater than the tabulated chi-square value. Therefore, the pattern of fossil preservation is dependent on location, suggesting that tectonics was the dominant factor in the formation of this fossil record, as originally suggested by Rogers (1993). However, a similar chi-square analysis (at the 5% level) of sites along a longitudinal transect in the distal regions of the Foreland Basin also shows that the calculated chi-square value is greater than the tabulated chi-square value. So, similar to the previous analysis, this shows that the pattern of fossil preservation is dependent on location. Given that in this second analysis the tectonic variable was held constant, this second analysis suggests that some other factor figured prominently in the patterns of preservation of the vertebrate fossil record in this basin.

DISCUSSION

In investigating the possible causal effects of a multitude of factors on a pattern, it is helpful if the

Table 3 Observed and expected values for the chi-square analysis to test independence of type of vertebrate fossil locality and geographic location. The expected values follow, in parentheses, the observed values in the table. The data are compiled from Dodson (1971), Brinkman (1990), Eberth (1990), Wood *et al.* (1988), Blob and Fiorillo (1996), Fiorillo and Currie (1994), and Fiorillo (1987a, 1987b, 1989, 1991a, 1997), as well as unpublished field notes of the author. The analysis was performed at 5% significance level, with 4 degrees of freedom. The calculated chi-square value is 13.9 and the expected value is 9.5. Because the calculated value is greater than the expected value, the null hypothesis, fossil type is independent of location, is rejected. Given that these data are from the part of the foreland basin distal to the basin axis, this result suggests that factors other than regional tectonism control the distribution of the types of vertebrate fossil locality. Table format follows examples from Rees (1989). Abbreviations: SCMT = south-central Montana; NCMT = north-central Montana; SAB = southern Alberta.

	Judith River Formation			
Type of bonebed	SCMT	NCMT	SAB	*N*
Lag	6(12.8)	10(12.2)	79(70)	95
Event	6(2.7)	3(2.6)	11(14.8)	20
Attritional	9(5.5)	7(5.3)	25(30.2)	41
N	21	20	115	

influence of some factors can be eliminated while examining others. In this investigation of the relative roles of climate and tectonics in the formation of the vertebrate fossil record of the Late Cretaceous foreland basin of the Rocky Mountain Region of western North America, the tectonic influence was reduced by examining three areas in the distal reaches of the basin. By holding the tectonic parameter constant, the chi-square analysis shows that mode of fossil preservation was dependent on location, obviously independent of tectonic setting. Therefore I conclude that the role of climate was significant (Figure 3), thereby supporting Brain's claim (1995) for the role of climate in the patterns of preservation.

But what is climate? Table 5 lists some of the broad-based categories that contribute to climate. For the purposes of this discussion I follow

Table 4 Summary of observed and expected values for the chi-square analysis to test independence of type of vertebrate fossil locality and geographic location. The expected values follow, in parentheses, the observed values in the table. The analysis was performed at 5% significance level, with 6 degrees of freedom. The calculated chi-square value is 82.1 and the expected value is 12.6. Because the calculated value is greater than the expected value, the null hypothesis, fossil type is independent of location, is rejected. Table format follows examples from Rees (1989). Abbreviations: SCMT = south-central Montana; NCMT = north-central Montana; SAB = southern Alberta.

	Judith River Formation			Two Medicine Formation	
Type of Bonebed	SCMT	NCMT	SAB		*N*
Lag	6(11.3)	10(10.3)	79(59)	0(14.9)	95
Event	6(5.0)	3(4.8)	11(27.4)	24(6.9)	44
Attritional	9(5.2)	7(5.0)	25(28.6)	5(7.2)	46
N	21	20	115		

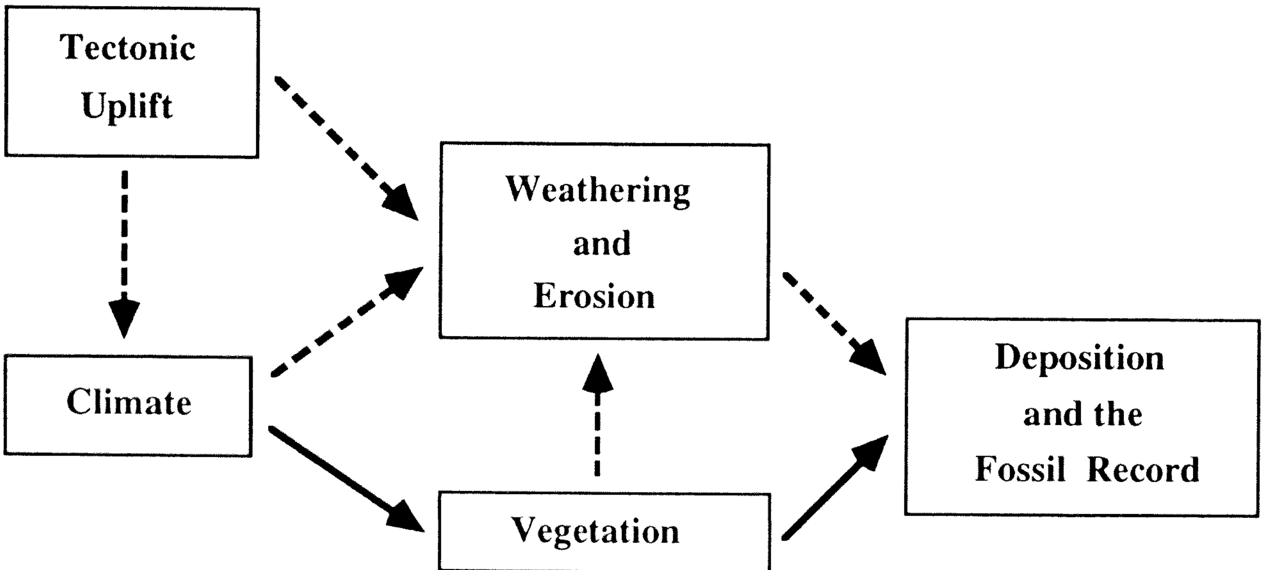

Figure 3 Potential interactions between the various parameters influencing the formation of the vertebrate fossil record in fluvial settings. Based on the analysis described in this study, the primary pathways for the formation of the vertebrate fossil record in the Late Cretaceous foreland basin of western North America are highlighted with solid black arrows, with the secondary pathways shown as dashed arrows.

Table 5 Summary of factors contributing to climate, based on the work of others such as Houghton *et al.* (1996). Of these factors, only the land-surface factors are considered in this discussion.

- Atmospheric Factors
  - Water Vapour
  - Clouds
    - Particle Size
    - Water Content
  - Precipitation
  - Convection
- Ocean Factors
  - Convection
  - Surface Fluxes
- Land-Surface Factors
  - Soil
    - Type
    - Moisture Content
  - Vegetation

Houghton *et al.* (1996) and their general perspective on climate, which is that it is the result of physical and biological factors that contribute to the overall system. These factors act either separately or through a feedback mechanism. It is beyond the scope of this paper to discuss more than the land surface factors of climate, and even then to only discuss some of these factors in a very broad sense.

As discussed in the Introduction, climate is a controlling influence on vegetative cover (Jenny 1941) and further, vegetative cover influences sediment yield (Leopold *et al.* 1964; Walling 1995, 1996). In examining river basin sediment yields, Walling (1996) succinctly pointed out that "sediment yields can be highly responsive to changes in erosion rates within their upstream catchments consequent upon changing land use or climate change". It has also been clearly shown that the type of vegetation can influence erosion rates (Keller and Swanson 1979; Keller and Tally 1979; Keller and MacDonald 1995; Smith 1976). Further, runoff is a function of soil moisture which varies with vegetative cover (Dickinson *et al.* 1996). Figure 4 highlights some of the factors contributing to runoff. Net rates of erosion, then, affect the patterns of deposition and the subsequent fossil record.

There is some evidence for changes in the rates of erosion in the rock record of the Late Cretaceous of this foreland basin. Variation in the sandstone-mudstone ratios (Table 1) is likely to be related to changes in runoff: increased abundance of mudstones probably indicating more complete, undisturbed vegetative cover and reduced erosion rates.

Is the geographic distance of several hundred kilometres between the localities in southern Alberta and those in southern Montana sufficient to invoke a change in climate and subsequent vegetative cover? Examination of the annual mean runoff maps provided by Starkel (1996) shows that variation in the Holocene along this same transect was at least 50 mm. Similarly, in monitoring temperature variation in this region in this century, there have been changes in the mean annual temperature gradient of 2°C (Nicholls *et al.* 1996). It

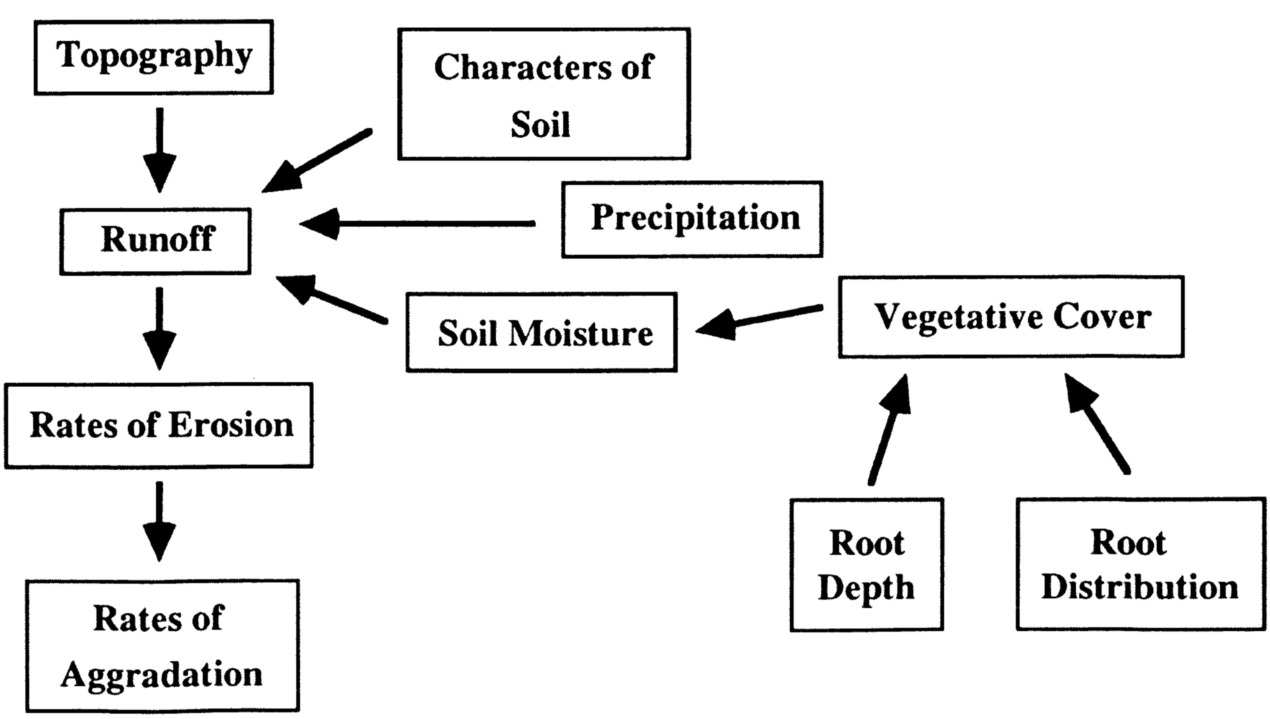

Figure 4 Summary of factors affecting runoff and the resulting rates of erosion and aggradation.

is not my contention that the same disparity existed in the Cretaceous; rather, this discussion would seem to confirm that this distance is sufficient for a measurable difference in some climatic variables. This difference was most likely reflected by some differences in the Cretaceous vegetative cover. This change in turn produced the variation in sandstone-mudstone ratios observed for these areas as well as differences in the frequency of the mode of taphonomic preservation. However, though this seems a sufficient explanation for the differences in the distribution of taphonomic modes for the tectonically distal parts of the basin, the upland Two Medicine Formation and the southern end of the distal transect in south-central Montana have identical sandstone-mudstone ratios.

Melillo *et al.* (1996) pointed out that changes in climate affect species composition and structure of ecosystems. Further, it has been suggested that the fossil faunas of southern Alberta and central Montana differ from those of south-central Montana (Fiorillo 1988b). The implication of this is that a climate-influenced factor, as yet undefined, contributed to the taphonomic differences observed between the Two Medicine Formation and the Judith River Formation of south-central Montana. Given that modern soils reflect a combination of factors related to climate, a detailed survey of fossil soils in each of these regions would likely prove insightful in analysing the inferred climate differences discussed here.

Whereas tectonics can play a prominent role in climate change, thereby altering rates of erosion (and subsequent deposition), variability in climate within a tectonic setting, without variation in tectonic regime, can also have a significant effect on rates of erosion and deposition. This conclusion suggests that patterns of fossil preservation are influenced by floodplain aggradation rates as a function of climate rather than regional tectonics. Given the microclimate variation that is readily observable in many modern settings, it seems that for the fossil record, developing a predictive model for regionally determining where particular types of vertebrate fossil concentrations can be found, is unlikely. In other words, this study suggests that the climate factors influencing the formation of the fossil record of vertebrates in the Late Cretaceous of Montana and Alberta were complex. Therefore, Rogers' (1993) generalization that the Judith River Formation is a rock unit appropriate for long-term ecological and evolutionary studies, while the Two Medicine Formation is appropriate for high-resolution ecological studies, appears too simplistic.

Further, there has been some discussion of comparing modes of taphonomic preservation of vertebrate remains from one formation to another (e.g. Dodson *et al.* 1980). This study illustrates that even within a rock unit there is significant taphonomic variability. Without an in-depth appreciation of the possible variation that may be present, formation-to-formation comparisons may be meaningless because taphonomic modes are controlled by small-scale factors that are capable of being variable within a formation, rather than large-scale tectonic differences between formations.

CONCLUSIONS

Both tectonics and climate have been demonstrated to be prominent factors in the formation of the sedimentological record. By extension, these factors must have been influential in the preservation of the vertebrate fossil record. The Late Cretaceous foreland basin of the Rocky Mountain region in North America, a rich source of vertebrate fossil remains, allowed investigation of this issue. A sample of 185 published and unpublished vertebrate localities was examined to determine the relative influence of regional tectonism versus climate in the formation of this fossil record.

The localities considered are all from the Judith River – Two Medicine clastic wedge in Montana and southern Alberta. A chi-square analysis of the distribution of these types of localities along a proximal-distal transect perpendicular to the long axis of the foreland basin shows that the pattern of fossil preservation is dependent on location, suggesting that tectonics was the dominant factor in the formation of this fossil record. However, a similar chi-square analysis of sites along a longitudinal transect in the distal regions of the foreland basin also shows that the pattern of fossil preservation is dependent on location. This pattern suggests that regional tectonism had a minor role in the formation of these deposits.

This dependency on location seems to relate closely to the sandstone/mudstone ratios of each region. These ratios are taken as indicators of rates of floodplain aggradation in the individual areas, which is controlled by variation in vegetative cover derived from climate. Based on this statistical analysis, it appears that large-scale tectonism is not a prominent influence in the formation of the vertebrate fossil record in the Late Cretaceous of western North America. Rather, for this basin, climatic variation played the dominant role.

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